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Standardized diet compositions and trophic levels of sharks

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Sharks are marine consumers believed to occupy top positions in marine food webs. But surprisingly, trophic level estimates for these predators are almost non-existent. With the hope of helping better define the ecological role of sharks in marine communities, this paper presents standardized diet compositions and trophic levels calculated for a suite of species. Dietary composition for each species was derived from published quantitative studies using a weighted average index that takes into account sample size in each study. The trophic level (TL) values of the 11 food types used to characterize the diet (obtained from published accounts) were then used to calculate fractional trophic levels for 149 species representing eight orders and 23 families. Sharks as a group are tertiary consumers (TL>4), and significant differences were found among the six orders compared, which were attributable to differences between orectolobiforms (TL<4) and all other orders, and between hexanchiforms and both carcharhiniforms and squatiniforms. Among four families of carcharhiniform sharks, carcharhinids (TL=4.1, n=39) had a significantly higher TL than triakids (TL=3.8, n=19) and scyliorhinids (TL=3.9, n=21), but not sphyrnids (TL=3.9, n=6). When compared to trophic levels for other top predators of marine communities obtained from the literature, mean TL for sharks was significantly higher than for seabirds (n=28), but not for marine mammals (n=97). Trophic level and body size were positively correlated (r_s=0.33), with the fit increasing (r_s=0.41) when the three predominantly zooplanktivorous sharks were omitted, and especially when considering only carcharhinid sharks (r_s=0.55).

Key words: trophic levels, diet composition, sharks, elasmobranchs, feeding ecology.

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Introduction

Sharks are believed to have played an important role in aquatic food webs throughout their evolutionary history. While it is widely recognized that many extant species of sharks are top or apex predators in marine communities, surprisingly little quantitative information is available on their diets. Furthermore, there are very few quantitative estimates of trophic levels to substantiate the claims of high trophic position of many species of sharks. As contemplated in the top-down view of ecological interactions (Brooks and Dodson, 1965), consumers can affect community structure and function. Many sharks, like marine mammals, are large and abundant marine consumers and as such are likely to influence the aquatic communities in which they exist (Bowen, 1997).

Two general approaches have been used to determine trophic levels in other marine organisms. Diet composition studies use the relative proportions of prey types and their respective trophic level (Mearns *et al.*, 1981; Sanger, 1987), whereas stable-isotope analysis provides estimates of assimilated foods based on measurements of stable isotopes of nitrogen and carbon in tissues of marine consumers (Fry and Sherr, 1988; Owens, 1988).

The goal of the present study was to calculate standardized diet compositions and to estimate trophic levels based on diets for all species of sharks for which quantitative studies were found. Both the dietary compositions and trophic levels obtained are species-specific and thus are intended to provide an integrated picture of each species in time and space.

Materials and methods

The target population of studies included all those which used an index to quantify stomach contents, or which

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Table 1. Prey categories used to calculate standardized diet compositions and trophic levels of sharks.

Code	Species group	Trophic level*
FISH	Teleost fishes	3.24
CEPH	Cephalopods (squids, octopuses)	3.2
MOL	Molluscs (excluding cephalopods)	2.1
CR	Decapod crustaceans (shrimps, crabs, prawns, lobsters)	2.52
INV	Other invertebrates (all invertebrates except molluscs, crustaceans, and zooplankton)	2.5
ZOO	Zooplankton (mainly euphausids "krill")	2.2
BIR	Seabirds	3.87
REP	Marine reptiles (sea turtles and sea snakes)	2.4
MAM	Marine mammals (cetaceans, pinnipeds, mustelids)	4.02
CHON	Chondrichthyan fishes (sharks, skates, rays, and chimaerids)	3.65
PL	Plants (marine plants and algae)	1

*Taken or calculated from Sanger (1987), Hobson and Welch (1992), Hobson (1993), Hobson *et al.* (1994), Pauly and Christensen (1995), and Pauly *et al.* (1998a).

provided sufficient dietary information to allow calculation of a quantitative index. Most of the work included consisted of peer-reviewed articles, but gray literature, unpublished theses and dissertations, some books, and in a few cases, personal communications, were also included. The Aquatic Sciences and Fisheries Abstracts (ASFA) and Biological Abstracts (BIOSYS) were the abstracting and indexing services utilized for systematic, computerized literature searches. Only studies published in this century were included and geographical coverage included all oceans and major seas.

Eleven food categories were considered to calculate standardized diet compositions and trophic levels of sharks (Table 1). An index of standardized diet composition was based on a weighted average that allows incorporation of data from multiple quantitative dietary studies of a particular species and takes into account the sample size (number of stomachs examined) in each study. The formula to calculate the proportion that each prey category P_j makes up of the diet is:

$$P_j = \frac{\sum_{i=1}^{n} P_{ij} N_i}{\sum_{j=1}^{11} \left(\sum_{i=1}^{n} P_{ij} N_i \right)}, \tag{1}$$

where P_{ij} is the proportion of prey category j in study i, N_i is the number of stomachs with food used to calculate P_{ij} in study i, n is the number of studies, j is the number of prey categories (11), and $\Sigma P_j = 1$.

For each study, P_{ij} values were calculated using the quantitative method used in the original study, with the following ranking criteria aimed at characterizing the diet more accurately: compound indices, such as the index of relative importance (IRI or %IRI), were used if available; otherwise, single indices, such as percent frequency of occurrence (%O), percent number (%N), percent weight (%W), or percent volume (%V) were used individually. If two single indices were available, an average was calculated (e.g. %N+%V/2). No qualitative data were used in this study. The complete list of references used to calculate diet compositions is not included owing to its extension, but is available from the author or from the Internet (Table 2).

Trophic levels (TL_k) were then calculated for each species (k) as:

$$TL_k = 1 + \left(\sum_{j=1}^{11} P_j \times TL_j \right), \tag{2}$$

where TL_j is the trophic level of each prey category j. Trophic level (TL) of prey categories was taken from several published accounts. The value for teleost fishes (Table 1) was the mean of 19 mean trophic levels calculated by Pauly and Christensen (1995) for several species groups, ranging from clupeids (TL=2.6) to scombrids (TL=4.2), using Ecopath II (Christensen and Pauly, 1992); values for all other prey categories, except seabirds, also came from Pauly and Christensen (1995) and Pauly *et al.* (1998a) and from Hobson and Welch (1992), who used stable-isotope analysis. Trophic level values for seabirds were taken from Sanger (1987), Hobson and Welch (1992), Hobson (1993), and Hobson *et al.* (1994) and refer mostly to seabirds found in polar ecosystems.

Trophic levels for families and orders were calculated as the mean of estimates for individual species. To evaluate the robustness of the conclusions to insufficient or poor data all calculations involving trophic levels were repeated after eliminating data for species with small sample sizes (n<20), with the exception of data for the three predominantly zooplanktivorous species (*Cetorhinus maximus*, *Rhincodon typus*, and *Megachasma pelagios*).

Table 2. Standardized diet compositions and trophic levels of sharks. See Table 1 for definitions of prey categories; n is the number of studies on which the estimates for each species are based, and N, the total number of stomachs analysed in all studies. Species are in alphabetical order within families. Summarized diet compositions from the original studies are available from the author as a MS Excel spreadsheet; a complete list of citations can be found online at: http://www.flmnh.ufl.edu/fish/Sharks/references/diet.htm

Species	n	N	FISH	CEPH	MOL	CR	INV	ZOO	BIR	REP	MAM	CHON	PL	Trophic level
Carcharhiniformes														
Carcharhinidae														
Carcharhinus acronotus	1	13	98.2	0.0	0.6	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
C. albimarginatus	2	15	75.0	12.5	0.0	0.0	6.3	0.0	0.0	0.0	0.0	6.3	0.0	4.2
C. altimus	3	22	43.3	13.4	0.0	3.3	3.3	0.0	0.0	0.0	0.0	36.7	0.0	4.3
C. amblyrhynchoides	2	164	89.3	2.9	0.0	4.9	0.0	0.0	0.0	0.0	0.0	2.9	0.0	4.2
C. amblyrhynchos	9	253	69.2	16.6	0.0	12.7	0.0	0.0	0.0	0.0	0.0	0.0	1.4	4.1
C. amboinensis	3	136	56.3	5.6	2.0	7.4	0.0	0.0	0.0	0.0	0.7	28.0	0.0	4.3
C. brachyurus	4	608	78.9	19.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	1.9	0.0	4.2
C. brevipinna	4	189	90.5	5.9	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.5	1.0	4.2
C. cautus	3	204	66.3	9.8	0.0	19.0	0.0	0.0	0.5	4.0	0.0	0.0	0.4	4.1
C. dussumieri	5	636	58.8	12.6	0.1	26.4	1.8	0.0	0.0	0.0	0.0	0.0	0.3	4.0
C. falciformis	9	47	63.8	32.7	0.0	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
C. fitzroyensis	2	55	72.4	1.7	0.0	25.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0
C. galapagensis	4	209	57.9	27.9	0.4	5.2	0.0	0.0	0.0	0.0	1.3	7.3	0.0	4.2
C. isodon	1	49	93.9	0.0	4.1	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	4.2
C. leucas	4	407	52.3	0.5	0.2	2.6	0.0	0.0	0.5	1.4	3.1	35.4	4.0	4.3
C. limbatus	11	1 180	88.9	4.1	0.2	2.1	0.1	0.0	0.0	0.0	0.0	4.5	0.1	4.2
C. longimanus	5	108	43.1	43.9	1.0	1.0	0.0	0.0	1.0	0.0	4.0	2.0	4.0	4.2
C. macloti	2	124	86.5	5.1	0.0	7.5	0.3	0.0	0.0	0.0	0.0	0.7	0.0	4.2
C. melanopterus	5	106	56.0	15.7	1.5	6.0	2.2	0.0	0.0	12.7	0.0	0.7	5.2	3.9
C. obscurus	5	468	58.5	22.8	1.3	4.7	0.0	0.0	0.0	0.0	0.6	12.0	0.0	4.2
C. plumbeus	7	1 273	55.0	13.3	0.0	25.3	0.0	0.0	0.0	0.0	0.1	6.3	0.1	4.1
C. porosus	1	171	85.7	0.0	0.0	14.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.1
C. sealei	1	16	52.7	36.8	0.0	10.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.1
C. signatus	1	1	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
C. sorrah	4	630	72.2	15.6	0.2	9.9	0.0	0.0	0.0	0.0	0.0	1.4	0.8	4.1
C. tilstoni	3	1 047	83.9	8.4	0.2	2.8	0.0	0.0	0.2	0.2	0.3	4.0	0.0	4.2
C. wheeleri	1	2	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
Galeocerdo cuvieri	13	1 209	35.4	4.8	0.6	12.2	0.2	0.0	10.4	23.8	4.6	8.0	0.1	4.1
Loxodon macrorhinus	1	207	48.3	11.9	0.6	38.3	0.9	0.0	0.0	0.0	0.0	0.0	0.0	3.9
Negaprion brevirostris	3	82	92.9	0.0	0.0	4.3	0.0	0.0	0.0	0.4	0.0	0.7	1.6	4.2
N. acutidens	7	271	84.4	3.6	2.4	8.5	0.0	0.0	0.0	0.0	0.0	0.0	1.1	4.1
Prionace glauca	14	1 293	38.5	49.4	0.2	5.0	1.0	4.9	0.3	0.0	0.2	0.4	0.2	4.1
Rhizoprionodon acutus	5	658	75.4	7.0	0.3	16.6	0.3	0.0	0.0	0.0	0.0	0.1	0.3	4.1
R. longurio	1	52	98.7	0.3	0.0	0.8	0.0	0.0	0.2	0.0	0.0	0.0	0.0	4.2
R. porosus	1	237	28.0	13.2	0.0	58.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8
R. taylori	3	258	84.1	0.4	0.0	15.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.1
R. terraenovae	2	109	66.4	1.8	0.1	31.6	0.0	0.0	0.0	0.0	0.0	0.1	0.0	4.0
Scoliodon laticaudus	1	415	33.3	5.9	0.0	60.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8
Triaenodon obesus	2	31	79.2	17.4	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2

Table 2. *Continued*

Species	n	N	FISH	CEPH	MOL	CR	INV	ZOO	BIR	REP	MAM	CHON	PL	Trophic level
Hemigaleidae														
Hemigaleus microstoma	3	396	1.0	93.8	1.4	2.6	1.0	0.0	0.0	0.0	0.0	0.2	0.0	4.2
Hemipritis elongatus	2	86	38.7	48.3	0.0	0.1	0.0	0.0	0.0	0.0	0.0	12.9	0.0	4.3
Proscyllidae														
Eridacnis radcliffei	1	277	67.7	3.6	0.0	28.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0
Gollum attenuatus	1	504	80.3	2.3	0.0	16.6	0.5	0.0	0.0	0.0	0.0	0.2	0.0	4.1
Pseudotriakidae														
Pseudotriakis microdon	2	14	67.9	13.3	0.0	0.0	0.0	0.0	0.0	0.0	8.3	10.4	0.0	4.3
Scyliorhinidae														
Apristurus brunneus	2	138	18.0	3.1	0.1	77.2	0.8	0.8	0.0	0.0	0.0	0.0	0.0	3.7
A. microps	1	64	21.5	23.5	0.0	53.3	0.8	0.0	0.0	0.0	0.0	0.9	0.0	3.8
A. saldanha	1	9	99.4	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
Cephaloscyllium isabellum	1	279	61.7	21.7	0.0	7.0	0.1	0.0	0.0	0.0	0.0	9.5	0.0	4.2
Cephalurus cephalus	1	9	20.0	0.0	0.0	70.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7
Galeus melastomus	7	3 716	32.9	3.8	0.0	32.3	14.4	16.5	0.0	0.0	0.0	0.0	0.0	3.7
G. murinus	1	2	50.0	25.0	0.0	0.0	0.0	25.0	0.0	0.0	0.0	0.0	0.0	4.0
G. polli	1	84	94.7	1.8	0.0	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
Halaelurus hispidus	1	184	85.6	6.4	0.0	8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
H. natalensis	2	2	29.3	70.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
Haploblepharus edwardsii	1	31	14.4	30.4	0.0	54.4	0.5	0.0	0.0	0.0	0.0	0.3	0.0	3.8
Holohalaelurus regani	1	291	68.4	22.1	0.0	9.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
Parmaturus xaniurus	1	70	6.7	0.1	0.0	91.0	0.0	2.2	0.0	0.0	0.0	0.0	0.0	3.6
Poroderma africanum	1	7	12.4	0.0	0.0	87.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6
Schroederichthys bivius	3	296	26.9	8.8	0.0	51.6	12.7	0.0	0.0	0.0	0.0	0.0	0.1	3.8
S. chilensis	1	201	0.4	0.0	0.0	99.3	0.2	0.0	0.0	0.0	0.0	0.0	0.1	3.5
Scyliorhinus canicula	7	7 555	17.2	4.2	21.5	42.0	14.7	0.0	0.0	0.0	0.0	0.1	0.0	3.6
S. capensis	1	97	69.0	2.0	0.0	25.8	3.2	0.0	0.0	0.0	0.0	0.0	0.0	4.0
S. meadi	1	1	33.3	33.3	0.0	33.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0
S. retifer	1	78	32.0	37.2	0.0	12.2	18.6	0.0	0.0	0.0	0.0	0.0	0.0	4.0
S. stellaris	3	1 426	29.5	43.8	0.2	22.1	4.2	0.0	0.0	0.0	0.0	0.2	0.0	4.0
Sphyrnidae														
Eusphyra blochii	1	287	82.9	4.0	0.0	12.8	0.0	0.0	0.0	0.0	0.0	0.3	0.0	4.1
Sphyrna lewini	13	1 253	61.9	15.5	0.1	22.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	4.1
S. mokarran	5	458	43.5	3.3	0.0	11.2	0.0	0.0	0.0	0.0	0.0	41.7	0.2	4.3
S. tiburo	3	482	1.6	2.2	0.0	71.5	0.0	0.0	0.0	0.0	0.0	0.0	24.6	3.2
S. tudes	1	39	16.7	0.0	0.0	83.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6
S. zygaena	6	243	29.8	68.9	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.9	0.0	4.2
Triakidae														
Galeorhinus galeus	5	68	79.2	16.4	0.0	1.1	2.1	0.0	0.0	0.0	0.0	1.1	0.0	4.2
Hypogaleus hyugaensis	1	2	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
Iago omanensis	3	257	44.4	44.2	0.9	9.7	0.7	0.0	0.0	0.0	0.0	0.0	0.0	4.1

Table 2. *Continued*

Species	n	N	FISH	CEPH	MOL	CR	INV	ZOO	BIR	REP	MAM	CHON	PL	Trophic level
Mustelus asterias	2	72	14.2	13.1	0.0	72.2	0.4	0.0	0.0	0.0	0.0	0.0	0.0	3.7
M. californicus	2	119	0.0	0.2	0.1	99.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	3.5
M. canis	4	211	16.6	0.0	5.3	64.3	13.8	0.0	0.0	0.0	0.0	0.0	0.0	3.6
M. fasciatus	1	2	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
M. henlei	3	138	15.9	3.0	0.0	69.6	8.9	0.0	0.0	0.0	0.0	0.0	2.6	3.6
M. higmani	1	74	6.9	2.7	0.0	89.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	3.6
M. lenticulatus	1	428	0.0	0.0	0.8	49.9	49.3	0.0	0.0	0.0	0.0	0.0	0.0	3.5
M. lunulatus	1	163	53.3	0.0	0.0	46.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.9
M. manazo	1	405	16.4	0.0	0.5	60.4	22.3	0.0	0.0	0.0	0.0	0.0	0.4	3.6
M. mustelus	3	452	13.1	31.6	0.0	54.7	0.6	0.0	0.0	0.0	0.0	0.0	0.0	3.8
M. palumbes	1	173	1.8	0.6	0.0	97.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	3.5
M. punctulatus	1	40	23.3	18.8	0.0	57.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8
M. schmitti	4	906	9.0	2.4	0.8	55.9	31.9	0.0	0.0	0.0	0.0	0.0	0.0	3.6
Scylliogaleus quecketti	1	11	0.0	11.0	0.0	89.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6
Triakis megalopterus	2	6	33.3	8.0	0.0	42.0	0.0	0.0	0.0	0.0	0.0	16.7	0.0	4.0
T. semifasciata	5	506	26.4	2.3	4.5	43.7	20.2	0.0	0.0	0.0	0.0	0.0	2.9	3.7
Lamniformes														
Alopiidae														
Alopias superciliosus	3	20	34.8	65.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
A. vulpinus	3	388	26.7	71.8	0.0	0.5	0.0	0.0	0.0	0.0	0.0	1.0	0.0	4.2
Cetorhinidae														
Cetorhinus maximus	3	11	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	3.2
Lamnidae														
Carcharodon carcharias	14	259	35.5	3.6	0.4	1.8	0.4	0.0	1.1	0.4	21.1	35.7	0.0	4.5
Isurus oxyrinchus	7	453	77.1	7.2	0.0	1.3	0.0	0.0	0.0	0.2	0.4	13.6	0.2	4.3
Lamna nasus	4	115	74.7	22.7	0.0	0.0	1.3	0.0	0.7	0.0	0.0	0.0	0.7	4.2
Megachasmidae														
Megachasma pelagios	4	4	0.0	0.0	0.0	28.6	28.6	42.9	0.0	0.0	0.0	0.0	0.0	3.4
Odontaspididae														
Carcharias taurus	5	70	65.9	2.9	0.0	0.1	0.0	0.0	0.0	0.0	0.0	31.2	0.0	4.4
Orectolobiformes														
Ginglymostomidae														
Ginglymostoma cirratum	3	16	25.0	19.4	0.0	55.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8
Nebrius ferrugineus	1	6	30.0	60.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.1
Hemiscyllidae														
Chiloscyllium griseum	1	78	30.3	2.3	7.8	33.5	26.1	0.0	0.0	0.0	0.0	0.0	0.0	3.7
Hemiscyllium ocellatum	1	38	0.3	0.0	0.0	54.1	45.6	0.0	0.0	0.0	0.0	0.0	0.0	3.5
Rhincodontidae														
Rhincodon typus	3	4	38.2	14.6	0.0	0.0	0.0	31.4	0.0	0.0	0.0	0.0	15.8	3.5

Table 2. *Continued*

Species	n	N	FISH	CEPH	MOL	CR	INV	ZOO	BIR	REP	MAM	CHON	PL	Trophic level
Stegostomatidae														
Stegostoma fasciatum	1	6	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.1
Hexanchiformes														
Chlamydoselachidae														
Chlamydoselachus anguineus	1	38	14.8	85.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
Hexanchidae														
Heptranchias perlo	2	13	40.0	40.0	0.0	13.3	0.0	0.0	0.0	0.0	0.0	6.7	0.0	4.2
Hexanchus griseus	4	106	22.9	57.0	0.3	0.0	0.0	0.0	0.0	0.0	8.9	10.7	0.0	4.3
H. vitulus	1	1	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
Notorynchus cepedianus	3	313	21.8	0.1	0.9	0.8	0.0	0.0	0.0	0.0	35.5	40.7	0.2	4.7
Pristiophoriformes														
Pristiophoridae														
Pliotrema warreni	1	10	80.0	10.0	0.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
Squatiniformes														
Squatinidae														
Squatina aculeata	1	20	47.4	15.8	0.0	36.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0
S. africana	1	11	71.4	28.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
S. argentina	1	53	80.4	2.0	0.0	17.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.1
S. californica	1	27	48.2	48.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6	4.1
S. oculata	1	14	61.0	8.5	0.0	30.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0
S. squatina	2	33	67.1	6.7	0.0	26.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0
Squaliformes														
Echinorhinidae														
Echinorhinus brucus	2	2	66.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	33.3	0.0	4.4
Squalidae														
Aculeola nigra	1	2	25.0	25.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.9
Centrophorus acus	1	15	84.2	7.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.9	4.1
C. granulosus	5	142	63.3	12.0	0.0	18.0	0.0	0.0	0.0	0.0	0.0	6.7	0.0	4.1
C. squamosus	4	41	65.7	34.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
Centroscyllium fabricii	5	56	26.3	10.9	0.0	62.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8
C. ritteri	2	144	18.6	5.7	0.6	2.3	0.0	72.8	0.0	0.0	0.0	0.0	0.0	3.5
Centroscymnus coelolepis	5	144	10.5	79.0	0.0	4.3	1.4	0.0	0.0	0.0	4.1	0.7	0.0	4.2
C. crepidater	2	17	42.7	48.5	0.0	8.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
Dalatias licha	4	226	56.1	9.8	0.0	17.2	2.4	0.0	0.0	0.0	0.0	14.6	0.0	4.1
Deania calcea	7	296	80.2	18.1	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
D. profundorum	2	58	81.8	18.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2

Table 2. *Continued*

Species	n	N	FISH	CEPH	MOL	CR	INV	ZOO	BIR	REP	MAM	CHON	PL	Trophic level
Etmopterus baxteri	1	117	70.6	26.9	0.0	2.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0	4.2
E. cf. brachyurus	1	62	77.7	17.1	0.0	5.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
E. compagnoi	1	15	46.9	46.4	0.0	6.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
E. cf. granulosus	2	54	18.0	60.8	0.0	21.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.1
E. lucifer	2	230	22.3	69.7	0.0	7.0	0.2	0.7	0.0	0.0	0.0	0.0	0.0	4.1
E. princeps	2	18	46.2	46.1	0.0	7.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
E. pusillus	1	5	40.0	60.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
E. spinax	7	1 461	33.3	19.7	0.0	22.7	0.5	23.8	0.0	0.0	0.0	0.0	0.0	3.8
E. unicolor	2	84	38.4	42.8	0.0	3.3	0.8	14.7	0.0	0.0	0.0	0.0	0.0	4.0
Euprotomicrus bispinatus	1	12	44.0	40.0	0.0	16.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.1
Isistius brasiliensis	2	68	32.0	52.0	0.0	4.0	0.0	0.0	0.0	0.0	12.0	0.0	0.0	4.3
Scymnodon ringens	1	1	50.0	0.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.9
Somniosus microcephalus	1	1	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
S. pacificus	6	13	33.3	38.9	5.6	5.6	0.0	0.0	0.0	0.0	16.7	0.0	0.0	4.2
S. rostratus	1	1	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2
Squalus acanthias	17	19 259	41.6	5.2	0.4	35.2	9.5	6.0	0.0	0.0	0.0	2.0	0.0	3.9
S. blainvillei	2	974	40.4	23.5	0.0	36.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0
S. cubensis	1	12	81.8	9.1	0.0	0.0	9.1	0.0	0.0	0.0	0.0	0.0	0.0	4.2
S. megalops	2	98	59.9	37.5	0.0	2.0	0.4	0.0	0.0	0.0	0.0	0.1	0.0	4.2
S. cf. mitsukurii	4	385	77.3	18.4	0.0	4.0	0.1	0.0	0.0	0.0	0.0	0.3	0.0	4.2
Heterodontiformes														
Heterodontidae														
Heterodontus francisci	1	97	0.0	0.1	71.3	27.0	0.2	0.0	0.0	0.0	0.0	0.0	1.4	3.2

Table 3. Trophic levels of sharks by order (in bold) and family.

Taxonomic group	n	Mean	LCL	UCL	Min	Max
Carcharhiniformes	90	4.0	3.9	4.1	3.2	4.3
Carcharhinidae	39	4.1	4.1	4.2	3.8	4.3
Hemigaleidae	2	4.2	4.1	4.3	4.3	4.3
Proscyllidae	2	4.1	4.0	4.1	4.0	4.1
Pseudotriakidae	1	4.3				
Scyliorhinidae	21	3.9	3.8	4.0	3.5	4.2
Sphyrnidae	6	3.9	3.6	4.2	3.2	4.3
Triakidae	19	3.8	3.7	3.9	3.5	4.2
Lamniformes	8	4.0	3.7	4.4	3.2	4.5
Alopiidae	2	4.2	4.2	4.2	4.2	4.2
Cetorhinidae	1	3.2				
Lamnidae	3	4.3	4.2	4.5	4.22	4.5
Megachasmidae	1	3.4				
Odontaspididae	1	4.4				
Orectolobiformes	6	3.6	3.4	3.9	3.1	4.1
Ginglymostomidae	2	4.0	3.8	4.2	3.8	4.1
Hemiscyllidae	2	3.6	3.5	3.8	3.5	3.7
Rhincodontidae	1	3.6				
Stegostomidae	1	3.1				
Hexanchiformes	5	4.3	4.2	4.5	4.2	4.7
Chlamydoselachidae	1	4.2				
Hexanchidae	4	4.3	4.2	4.5	4.2	4.7
Pristiophoriformes	1	4.2				
Pristiophoridae	1	4.2				
Squatiniformes	6	4.1	4.0	4.2	4.0	4.2
Squatinidae	6	4.1	4.0	4.2	4.0	4.2
Squaliformes	32	4.1	4.0	4.2	3.5	4.4
Echinorhinidae	1	4.4				
Squalidae	31	4.1	4.0	4.2	3.5	4.3
Heterodontiformes	1	3.2				
Heterodontidae	1	3.2				

n is number of species; LCL and UCL are 95% lower and upper confidence limits of the mean; Min is minimum value, Max is maximum value.

Results

Standardized diet compositions and trophic levels were calculated for 149 species of sharks (Tables 2 and 3). The histogram of estimated trophic levels of sharks shows that the distribution is not normal (Kolmogorov-Smirnov test, $p<0.001$; Fig. 1). Descriptive statistics (Table 4) indicated that sharks as a group are predominantly tertiary consumers (TL>4), but orectolobiforms (n=6) and heterodontiforms (n=1) are secondary consumers (TL<4). There were significant differences in TL among six orders compared statistically (Kruskal-Wallis test on ranks corrected for ties, 5 d.f., $p=0.002$; Fig. 2). *Post hoc* multiple-comparison Z-value tests further indicated that orectolobiforms, the only group compared with mean TL<4, were significantly different from the other five orders analysed, and hexanchiforms (n=5), the group with the highest TL (4.3), were also significantly different from both carcharhiniforms (TL=4.0, n=90) and squatiniforms (TL=4.1, n=6).

The trophic levels ranged from 3.1 in the zebra shark, *Stegostoma fasciatum* (Orectolobiformes) to 4.7 in the broadnose sevengill shark, *Notorynchus cepedianus* (Hexanchiformes) (Table 2). The second highest TL (4.5) corresponded to the great white shark, *Carcharodon carcharias* (Lamniformes).

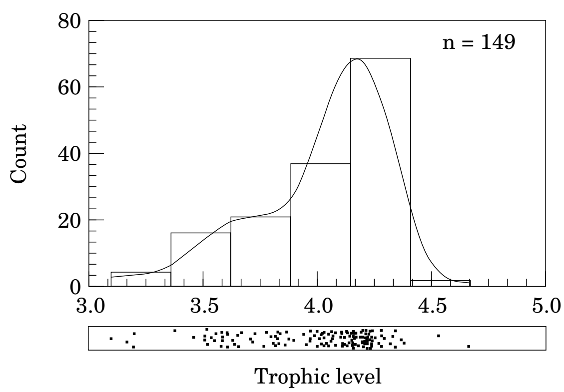

Figure 1. Histogram of trophic levels of sharks. Also shown are the density trace and dot plot.

Table 4. Descriptive statistics of trophic levels of sharks, marine mammals, and seabirds. Values for marine mammals were calculated from data in Pauly *et al.* (1998a) and exclude sirenians, freshwater dolphins, and polar bears; values for seabirds were calculated from Sanger (1987), Hobson and Welch (1992), Hobson (1993), and Hobson *et al.* (1994).

Taxonomic group	N	Mean	LCL	UCL	Min	Max	Median	25%p	75%p	Mode
Sharks	149	4.0	4.0	4.1	3.1	4.7	4.1	3.8	4.2	4.2
Marine mammals	97	4.0	3.9	4.1	3.2	4.5	4.1	4.0	4.3	4.1
Seabirds	28	3.9	3.7	4.0	3.1	4.8	3.8	3.6	4.1	4.1

LCL and UCL are 95% lower and upper confidence limits of the mean; 25%p and 75%p are the 25th and 75th percentiles of the median.

Statistical comparison of TL values calculated for four families of carcharhiniform sharks for which sample size was reasonably high (Table 3) revealed significant differences (Kruskal-Wallis test on ranks corrected for ties, 3 d.f., $p=0.00005$). *Post hoc* multiple-comparison Z-value tests indicated that carcharhinids ($n=39$), the only family of the four analysed with mean $TL>4$, were significantly different from triakids ($TL=3.8$, $n=19$) and scyliorhinids ($TL=3.9$, $n=21$), but not from sphyrnids ($TL=3.9$, $n=6$).

Trophic levels of sharks were compared to values for mammals presented in Pauly *et al.* (1998a), which excluded sirenians, freshwater dolphins, and polar bears, and to values for seabirds presented in Sanger (1987), Hobson and Welch (1992), Hobson (1993), and Hobson *et al.* (1994) (Table 4). A Kruskal-Wallis test on data corrected for ties revealed significant differences among the three groups (2 d.f., $p=0.023$), with *post hoc* multiple-comparison Z-value tests indicating that sharks

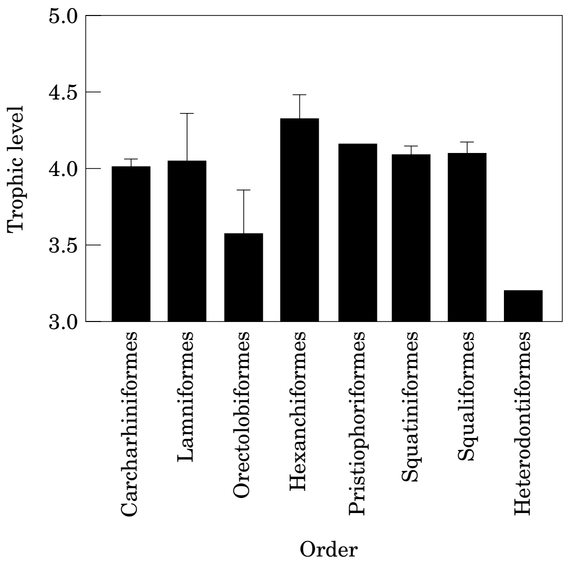

Figure 2. Trophic levels for eight orders of sharks. Values shown are means with upper 95% confidence limits, except for pristiophoriformes ($n=1$) and heterodontiformes ($n=1$).

($n=149$) and marine mammals ($n=97$) were significantly different from seabirds ($n=28$). Mean TL for marine mammals and sharks as a group was identical (Table 4).

Trophic level and body size (total length) were positively correlated (Spearman rank correlation coefficient, $r_s=0.33$, $p<0.0001$, $n=149$; Fig. 3a), with the fit increasing ($r_s=0.41$, $p<0.0001$, $n=146$; Fig. 3b) when the three predominantly zooplanktivorous species were removed. Trophic level and body size showed a stronger correlation in carcharhinid sharks ($r_s=0.55$, $p=0.0003$, $n=39$; Fig. 3c), with a monomolecular curve of the type $TL=A(1-e^{-kL})$, where A is an asymptote, k is a rate constant, and L is total length in cm, giving a good fit to the data (Pearson correlation coefficient, $r=0.56$, $p<0.001$, $n=39$).

Repetition of the analyses after eliminating species with small sample sizes resulted in no appreciable changes in results. Mean TL for sharks ($n=112$) was still 4.0 and there were no significant differences in TL among the three orders (carcharhiniforms, lamniforms, and squaliforms) that could be compared statistically. Statistical differences among the four carcharhiniform families compared remained the same as in the baseline analysis. Differences among sharks, marine mammals, and seabirds also remained the same, albeit a little less significant ($p=0.032$), and trophic level and body length were more positively correlated in all cases.

Discussion

The findings of this study support the common view that sharks are top predators. Mean trophic level for sharks was identical to that calculated for marine mammals, although the latter did not include sirenians, which are herbivores ($TL=2$); freshwater dolphins, which are not marine; and polar bears ($TL=5.1$; Hobson and Welch, 1992; Pauly *et al.*, 1998a). However, this study indicates that trophic levels of sharks are somewhat higher than those of seabirds obtained from the literature, calculated using both dietary and stable-isotope analyses. These results generally suggest that sharks utilize similar resources to these other high-level marine consumers.

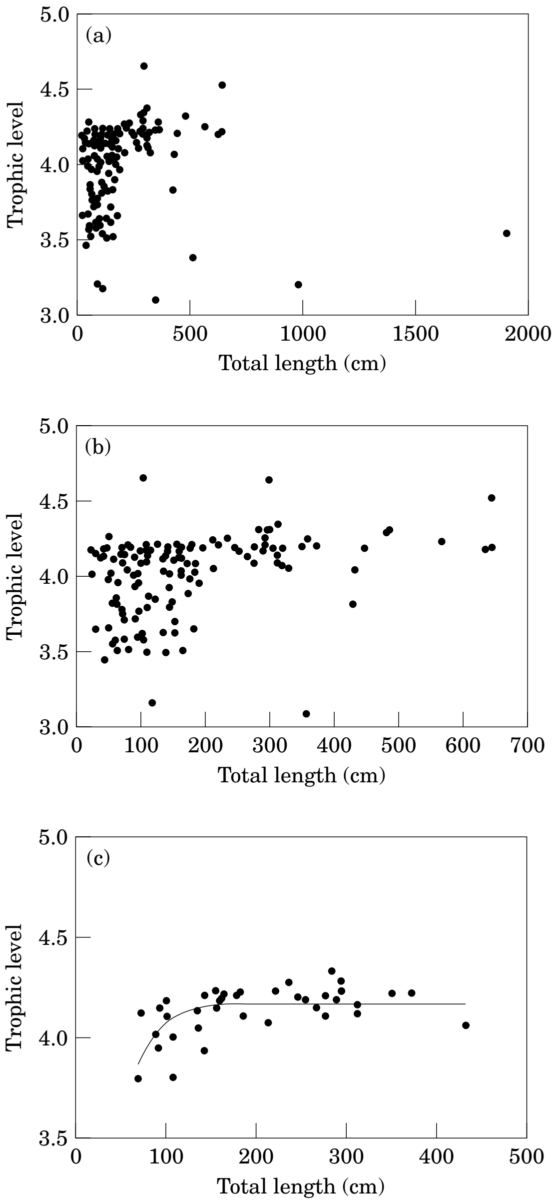

Figure 3. Relationship between total length and trophic level of sharks. (a) is for 149 species representing eight orders and 23 families, (b) does not include the three predominantly zooplanktivorous species, and (c) is for 39 species of carcharhinid sharks only.

Trophic levels estimated here agree well with several values reported by Opitz (1996) for sharks and rays of Caribbean coral reef ecosystems, which ranged from 3.9 to 4.1. These values, also calculated using Ecopath II, were based on food consumption estimates for 13 species of sharks (9 carcharhinids, 1 ginglymostomid, 2 sphyrnids, and 1 triakid) and two species of rays (1 dasyatid and 1 myliobatid).

Body length and trophic level were moderately correlated. It is possible that body mass could have been a better predictor, but this variable was not available for many species, hence the use of body length as a surrogate. Even in the case of carcharhinid sharks, which showed the highest correlation, only 30% of the variance was explained by trophic level and body length. The positive trend between body length and trophic level contradicts the view that trophic levels of aquatic organisms are inversely related to size (Pauly *et al.*, 1998b and references therein).

There are a number of factors which may have affected the TL values found in this study. The weighted average index was intended to favour those studies conveying the most information, and thus incorporated weights for the number of stomachs with food examined in each study. While different single or combined indices of dietary analysis provide different types of information and may be incommensurable (Cortés, 1997), it would have been too limiting to use only one specific method and so a variety of indices were included to calculate the weighted average index. It was also deemed preferable not to include qualitative dietary descriptions or behavioural observations to avoid further imprecision and bias in the estimates.

Trophic level of prey may also have affected estimates. In particular, the value used for fishes incorporated a wide array of teleost species, albeit the majority were secondary consumers (TL>3). It would have been preferable to use narrower groupings, as for example, in Pauly *et al.*'s (1998a) division of fishes into small pelagic, mesopelagic, and miscellaneous fishes. However, this would have also prevented use of a considerable number of studies in which prey items were only described as "fish".

It is expected that more detailed, species-specific or population-based studies will yield different diet compositions and trophic levels from those found in the present study. However, it is felt that the magnitude of this discrepancy should not be very large. Standardized diet compositions and trophic levels presented herein should be regarded as aggregates that provide an integrated description for each species including variability among populations in time and space. These estimates should also be considered preliminary and dynamic, in as much as additional dietary studies will provide more information that can be incorporated into the quantitative index to fine-tune the estimates.

The aim of the dietary composition approach was to include as many quantitative studies as possible. As a corollary, the resulting estimates may be biased in some cases because not all studies used to calculate the index were equally reliable. However, further weighting by a reliability scale would have been too subjective and it was decided not to include it. Trophic levels estimated for families, orders, and sharks as a group were robust to the influence of species with small sample sizes and indeed none of the conclusions based on the whole data set (n = 149) changed after eliminating those species (n = 149 − 37 = 112). The robustness and imprecision of the diet composition and trophic level estimates could be further evaluated by using resampling techniques, such as the bootstrap, or Monte Carlo simulation as proposed by Pauly *et al.* (1998a), but this was beyond the scope of the present work.

It appears that the marine food webs in which sharks exist are considerably long, with at least four trophic levels in many cases, and with sharks generally occupying the upper trophic positions. It is unclear what effect this can have on community stability, especially in the light of recent findings disputing the long-held view that longer food chains are more dynamically fragile thereby limiting food chain length (Sterner *et al.*, 1997). While it is intuitively easy to predict that high-order carnivores such as sharks exert top-down effects, these putative effects remain very poorly understood and unquantified. Similarly, bottom-up effects of lower trophic level organisms in the overall processes of energy transfer ultimately reaching sharks are virtually unknown. Despite this uncertainty, the high trophic levels of sharks suggest that overall yield from fisheries should be low and not sustainable at high exploitation levels, as seen for other high trophic level fishes (Pauly *et al.*, 1998b).

It is widely recognized that establishing trophic relationships within communities is a daunting task (Paine, 1988; Hobson and Welch, 1992). This is particularly true of marine communities and of the upper-level consumers, such as sharks, within them. The main reasons for this are logistical limitations, such as the difficulty of year-round sampling in marine ecosystems or the extreme difficulty and sometimes impossibility of conducting manipulative experiments with large organisms, such as marine mammals (Bowen, 1997) or sharks (Cortés, 1997). Owing to these limitations to both temporal and spatial scaling, studies of trophic organization dealing with sharks will likely continue to depend to a large extent on punctual stomach content analyses, because they remain simpler and less time-consuming than stable-isotope analyses. However, it is highly desirable that much more attention be focused on the stable-isotope approach at least as a validation of conventional dietary analyses.

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References

Bowen, W. D. 1997. Role of marine mammals in aquatic ecosystems. Marine Ecology Progress Series, 158: 267–274.

Brooks, J., and Dodson, S. I. 1965. Predation, body size, and composition of plankton. Science, 150: 28–35.

Christensen, V., and Pauly, D. 1992. The ECOPATH II – a software for balancing steady-state models and calculating network characteristics. Ecological Modelling, 61: 169–185.

Cortés, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Canadian Journal of Fisheries and Aquatic Sciences, 54: 726–738.

Fry, B., and Sherr, E. B. 1988. δ13 C measurements as indicators of carbon flow in marine and freshwater ecosystems. *In* Stable isotopes in ecological research, pp. 196–229. Ed. by P. W. Rundel, J. R. Ehleringer, and K. A. Nagy. Springer Verlag, NY.

Hobson, K. A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Marine Ecology Progress Series, 95: 7–18.

Hobson, K. A., and Welch, H. E. 1992. Determination of trophic relationships within a high Arctic marine food web using δ^{13} C and δ^{15} N analysis. Marine Ecology Progress Series, 84: 9–18.

Hobson, K. A., Piatt, J. F., and Pitocchelli, J. 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology, 63: 786–798.

Mearns, A. J., Young, D. R., Olson, R. J., and Schafer, H. A. 1981. Trophic structure of the cessium-potassium ratio in pelagic ecosystems. California Cooperative Oceanographic and Fisheries Investigation Report, 22: 99–110.

Opitz, S. 1996. Trophic interactions in Caribbean coral reefs. ICLARM Technical Report, 43. 341 pp.

Owens, N. J. P. 1988. Natural variations in 15N in the marine environment. Advances in Marine Biology, 24: 389–451.

Paine, R. T. 1988. Food webs: road maps of interactions or grist for theoretical development? Ecology, 69: 1648–1654.

Pauly, D., and Christensen, V. 1995. Primary production required to sustain global fisheries. Nature, 374: 255–257.

Pauly, D., Trites, A., Capuli, E., and Christensen, V. 1998a. Diet composition and trophic levels of marine mammals. ICES Journal of Marine Science, 55: 467–481.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F., Jr. 1998b. Fishing down marine food webs. Science, 279: 860–863.

Sanger, G. A. 1987. Trophic levels and trophic relationships of seabirds in the Gulf of Alaska. *In* Seabirds: Feeding ecology and role in marine ecosystems, pp. 229–257. Ed. by J. P. Croxall. Cambridge University Press, Cambridge.

Sterner, R. W., Bajpai, A., and Adams, T. 1997. The enigma of food chain length: absence of theoretical evidence for dynamic constraints. Ecology, 78: 2258–2262.